THE RECOGNITION OF SALINITY-CONTROLLED MOLLUSC ASSEMBLAGES IN THE GREAT ESTUARINE SERIES (MIDDLE JURASSIC) OF THE INNER HEBRIDES

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Abstract. The Great Estuarine Series was deposited in large, shallow lagoons. Its abundant molluscan faunas are restricted to very few genera and species, several of which are similar to modern fresh- and brackish-water forms. Consideration of the nature and history of the brackish-water fauna, together with direct comparison with the modern brackish-water environments of the Texas coast, results in an interpretation of the faunas as being controlled very largely by salinity variations in time. The salinities ranged from freshwater to fully marine, but were usually intermediate.

The purpose of this paper is to show that the molluscan faunas of the Great Estuarine Series lived in brackish waters in a lagoonal environment, and that it is possible to recognize a series of overlapping faunal assemblages whose composition and distribution were controlled largely by salinity variations in time. The detailed evidence on which this thesis is based, the stratigraphical distribution of the faunas, and the ecology of the fossils concerned, is described in a second paper (this journal, p. 327).

THE GREAT ESTUARINE SERIES

The stratigraphy of the Great Estuarine Series (Upper Bajocian–Bathonian) has been described elsewhere (Hudson 1962); the Staffin Bay Beds (Upper Bathonian?–Lower Callovian) of Trotternish are not now included in the Great Estuarine Series. The 'Series' has long been recognized as of unusual facies, 'estuarine' in the wide sense of nineteenth-century geologists (Judd 1873, 1878), since it bears unmistakable signs of deposition in very shallow water, and has a fauna which is impoverished in numbers of species but very abundant in numbers of individuals.

Depositional environment. The conditions of deposition of the Great Estuarine Series naturally varied from one formation to another, but some generalizations can be made. The characteristic feature of all the shale and limestone formations is that lithologies and faunas may vary very rapidly from bed to bed up the succession, but are laterally persistent; some beds can be traced for several miles. There is abundant evidence of very shallow-water conditions throughout, with frequent mudcracked surfaces, but the area never became a land surface. These features, together with the brackish-water nature of the fauna, are best explained if deposition was in extensive shallow lagoons, probably partially separated by a bar from the open sea. The sandy formations represent the subaqueous portions of deltas built into these lagoons, which persisted throughout the deposition of the 'Series'. Such lagoons are very favourable to the establishment of more or less stable brackish-water conditions; the best modern examples—the bays of the Texas coast—are discussed below.

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Nature of the fossil assemblages. Most of the fossils of the Great Estuarine Series are not in position of life. They occur as accumulations of dead shells, probably winnowed by wave action, with the valves of lamellibranchs disarticulated. However, the shell beds are enclosed in fine-grained shales, and there is seldom any evidence of strong currents or of long distance derivation. So that, although the shell beds are death assemblages, they are indigenous death assemblages in the sense of Hallam (1960), and represent the general environment in which they are found, though small-scale patchiness of distribution may have become blurred. The uniformity of composition of many of the shell beds, especially some of the more obviously drifted ones, supports this interpretation; and adjacent shell beds, separated by only a few inches of shale, may have different compositions. There is much less need to invoke faunal mixing to explain assemblages than might be expected.

SOME ASPECTS OF BRACKISH WATER FAUNAS

The chemical and biological classification of brackish waters has been reviewed by Hiltermann (1949); and Table 1 is slightly modified from his paper. The biological classification is based mainly on the work of Remane at Kiel (see below); it assumes, of course, reasonable constancy of other environmental conditions. When used of conditions (e.g. brackish lagoon), the word 'brackish' usually implies a fairly stable intermediate salinity, contrasted with the tidally fluctuating salinity of an estuary, but never as stable as that of the sea. The following discussion on modern brackish-water faunas is based mainly on review articles on the fauna in general (Gunter 1947, Hiltermann 1949, Schmidt 1951, Pearse and Gunter 1957, Hedgpeth 1957) and on special areas (Segerstråle 1957, Sorgenfrei 1958 on the Baltic, Ladd *et al.* 1957, Parker 1959, Shepard *et al.* 1960 on Texas coast bays).

TABLE 1. *Classification of brackish water. Mainly after Hiltermann (1949)*

Biological classification (mainly after Remane)	*Descriptive term*	*Total salinity (parts per thousand)*
Freshwater	Freshwater	0–0·5
Freshwater province with reduced number of species	Oligohaline brackish water	0·5–3
Brackish freshwater	Miohaline brackish water	3–5
Typical brackish water	Mesohaline brackish water	5–9
Brackish-marine	Pliohaline brackish water	9–16·5
Marine province with reduced number of species	Brachyhaline sea water	16·5–30
Marine	Sea water	30–40
(Not considered by Remane)	Hypersaline water	greater than 40

The most obvious and well-known characteristic of brackish-water faunas, whether stable-brackish or estuarine, is their paucity in numbers of species, contrasted frequently with great abundance of individuals. Temperature effects, oxygen deficiency, and extreme exposure to waves can cause a similar restriction, but can frequently be eliminated as an important cause by regional studies (Sorgenfrei 1958). The explanation of this effect is that, while brackish waters are often rich feeding grounds, few animals are able to use them because of physiological difficulties, mainly of osmoregulation, so that those few which have overcome the difficulties multiply greatly.

Two other points from the literature are relevant:

1. Even at quite low salinities the brackish-water fauna is predominantly reduced-marine; hence the minimum number of species is found, not midway between marine salinity and freshwater, but at a salinity of around 5–9‰. This was first established by Remane at Kiel, and the general result seems to be accepted (Hedgpeth 1957, pp. 702–3).

2. The brackish-water fauna is recruited from a small part only of the marine fauna. Whole phyla or other major taxa are stenohaline (corals, echinoderms, cephalopods, articulate brachiopods). Even among the molluscs and the crustaceans, which are the most important groups in brackish waters today, only a few relatively small groups produce brackish-water forms in any numbers.

Rapid fluctuations in salinity are more deadly to marine animals than slow ones; hence, for a given gradient of average salinities, estuaries will show a sharper faunal reduction than stable brackish waters. Stable brackish waters are also more liable to invasion, at low salinities, by freshwater forms (e.g. *Unio* at salinities of up to 3–4‰ in the Baltic area). Many animals of brackish lagoons also live in near-by hypersaline ones. 'This suggests that once an organism is capable of adjusting itself to salinity changes its range of tolerance may exceed the usual changes in its immediate environment, so that salinity is not the governing factor and the organism is able to meet unusual conditions, and colonise extreme environments' (Pearse and Gunter 1957, p. 147).

This may also help to explain the second observation, that the brackish-water fauna comes from only a few invertebrate taxa. Few organisms seem actually to require the fluctuating conditions always associated with low salinity, but once an organism can withstand them it has a permanent advantage in an evolutionary sense (Hedgpeth 1957, p. 695). Since brackish-water animals can by definition withstand large short-period oscillations, usually of temperature and depth as well as of salinity, they are better equipped to withstand small secular changes than animals adapted to a narrower range of conditions. These less-adaptable animals must either evolve distinct features to encounter the changed environment, or become extinct. Therefore estuarine (and brackish-water) species are often conservative forms with a long history (Hedgpeth 1957, p. 696). Hedgpeth quotes the oysters as a typical case, and concludes that 'euryhalinity runs in families'.

Hutchinson (1960) makes the further point that freshwater faunas, too, are very long-ranging. He estimates that only 20–30 separate invasions from the sea are required to account for all the flourishing molluscan faunas of modern lakes and rivers. Their inability to re-enter any but the most dilute of brackish waters makes these freshwater forms extremely valuable environmental indicators.

The recognition of fossil brackish-water faunas. An admirable review of this problem has been given by Schmidt (1951). This has the encouraging result of reaffirming most of the traditional criteria for brackish water; Schmidt concludes that the following four criteria should be diagnostic of fossil brackish-water faunas, and hence deposits.

1. Paucity of species, often forming monotypic shell beds.
2. Absence of stenohaline groups.
3. Presence of euryhaline animals, including special brackish-water forms, notably lamellibranchs (and also some gastropods) among the macrofauna, and, among the hard-shelled microfauna, particularly ostracods.

4. Association of marine and freshwater (not hypersaline) deposits. This means considering the palaeogeography, e.g. hypersaline deposits should be associated with evaporites, true brackish deposits with deltaic sands and drifted plant remains.

Among general conditions mentioned by Schmidt as favourable for the production of brackish-water areas are a wet climate in the source area, leading to high run-off; and in the depositional area, leading to small evaporation. The absence of strong sea currents near the river mouths is favourable; hence lagoons and restricted gulfs are often brackish. If brackish water is deduced from other considerations, those conditions are correspondingly indicated, a fact which is obviously useful in palaeogeography. Schmidt gives a review of brackish-water faunas and sediments in the stratigraphical column, and remarks that their recognition back, as he claims, to the Lower Palaeozoic suggests that the salt sea is very ancient. As a result of their review, Pearse and Gunter (1957, pp. 131–3) also conclude that the salinity of the open ocean has been fairly constant. For the following discussion, which is mainly concerned with relative salinity, it will therefore be assumed that the Jurassic ocean, like the modern one, had a salinity of 35‰.

THE GREAT ESTUARINE SERIES AS A BRACKISH-WATER DEPOSIT

The Great Estuarine Series, taken as a whole, admirably fits Schmidt's criteria for a brackish-water deposit.

1. The total number of macro-invertebrate species recorded is less than 50, compared with over 200 species each of gastropods and lamellibranchs as well as numerous brachiopods, echinoderms, &c., from the English Great Oolite (Cox and Arkell 1948–50). This result is too extreme to be explained entirely by deficient collecting. Monotypic shell beds are extremely characteristic.

2. A few feet of strata in the Lower Ostrea Beds are responsible for nearly all records of stenohaline forms from the Series—one echinoid plate and spine, one polyzoan, one species of articulate brachiopod, a few records of foraminifera. Corals and cephalopods are completely unknown.

3. Lamellibranchs, less often gastropods, ostracods, and *Euestheria* (*Estheria* auct.), or some combination of these groups, dominate the fauna at all horizons. They include several well-known brackish-water forms.

4. Marine beds occur above and below the Series; one or two freshwater beds occur within it. Drifted plant remains are common in the sandstones. Evaporites are absent throughout the British Middle Jurassic, and plant remains and deltaic deposits are common.

The conclusion that the Great Estuarine Series is a brackish-water deposit is not new; Hugh Miller (1858, especially p. 55) has a very well-argued passage on the subject. It has been deduced without subdividing the Series, and without considering the fauna except in the most general terms of phyla and classes.

The appropriate taxonomic level at which to discuss the fauna in more detail is that of rather broad genera. It is immediately striking that, of the small total number of genera in the Great Estuarine Series, several are still living in brackish or fresh waters; they are plausibly regarded as members of those conservative euryhaline or freshwater groups discussed above. *Liostrea* (*Ostrea* s.l.), *Mytilus*, *Unio*, *Viviparus*, and *Euestheria* are the best known. Not only do all these occur in the same group of rocks, which in itself strengthens the 'conservative' hypothesis, but when separate formations are considered, and still more when the rocks are examined bed by bed, it is found that they do not occur indiscriminately mixed. *Liostrea hebridica* and *Mytilus strathairdensis*, which are members of marine-euryhaline genera, both occur most typically in monotypic shell beds, recalling modern oyster and mussel beds. *Liostrea* also occurs in the marine horizon mentioned above, with genera usually regarded as fully marine (*Rhynchonella*, *Myopholas*, *Anisocardia*) in assemblages very similar to those of the fully marine Great Oolite. *Unio* and *Viviparus*, on the other hand, which are freshwater at the present day, do not occur with the marine genera, nor with *Liostrea* or *Mytilus*, but they do occur together. Their other main associate is the extinct lamellibranch *Neomiodon*, which forms with *Unio* and *Viviparus* the well-known Hastings Beds assemblage of the Wealden, which has always been regarded as freshwater. *Neomiodon*, however, also occurs with the more marine genera mentioned above. It seems to have been euryhaline, though as usual with such forms it is most abundant numerically in low-salinity assemblages, often forming monotypic shell beds. A frequent associate of *Neomiodon* and *Viviparus* is *Euestheria*, which inhabits fresh or rarely brackish water today. Ostracods are also most abundant in the beds with *Euestheria* and *Neomiodon*.

It is therefore possible to divide the Great Estuarine Series assemblages at least into more and less saline, as briefly indicated by Anderson (1948) and others, and perhaps to arrange them in a salinity series. On the whole the Estheria Shales, the Concretionary Sandstone Series, and the Ostracod Limestones have a low-salinity fauna, and the Lower Ostrea Beds and the Staffin Bay Beds (= Upper Ostrea Beds and Belemnite Sands, of Anderson and Cox 1948) a high-salinity one. The Mytilus Shales, and parts of the Estheria Shales and Lower Ostrea Beds, show rapid alternations within a few feet (or sometimes a few inches) from one type of fauna to the other, within a fairly constant gross lithology. These reversed and repeated changes rule out evolution or long-range immigration as explanations of the faunal changes, and render large changes of depth most improbable. Salinity changes seem much the most reasonable explanation. Salinity-controlled assemblages of similar type are known in the Baltic and in the Texas Bays, where conditions more closely approach those envisaged for the Great Estuarine Series.

THE TEXAS COAST BAYS AND THEIR MOLLUSCAN FAUNA

These bays have been intensively studied in the last few years, and the results have now been collected and summarized in Shepard *et al.* (1960). The earlier reports most relevant to the present topic are by Ladd *et al.* (1957) and Parker (1959). The situation is intermediate between that in large masses of stable brackish water, such as the Baltic, and that in a typical estuary.

The bays form a complex series of estuaries and lagoons behind a string of sandy barrier islands, through which are narrow connexions to the Gulf of Mexico. The climate in the area varies from humid in the north-east, near the Mississippi delta, to semi-arid in the south-west. The whole system is extremely shallow, less than 9 ft., but the bays rarely dry up. Tides are negligible. The total salinity variation is large, from virtually fresh to hypersaline, but in any one part of the system may be constant for several years. A typical pattern is a slow build-up to high salinities in a spell of dry years, leading to an invasion of marine forms, followed by sudden freshwater floods. These have been recorded as reducing salinities from 40‰ to 2–4‰ in a few weeks, causing mass-mortalities of the marine forms. The sediment is mainly mud, stratified in the bay heads where the fauna is sparse, structureless in the lower bays. The sediment of the barrier islands and passes is more sandy and contains echinoid remains.

The distribution of both micro- and macrofaunas is controlled very largely by salinity, or at least parallels the salinity contours. Minor variations due to the nature of the bottom, &c., are superimposed on this salinity-controlled pattern. The fauna of the waters of very low salinity is very poor in numbers of species, and the change from this to the 'mid-estuarine' fauna inhabiting waters of about half the salinity of sea water is much sharper than the change from the mid-estuarine to the marine fauna. This accords with Remane's observations in the very different environment of the Baltic.

The macro-invertebrate assemblages (especially of the molluscs), as described by Parker (1959), are of great interest. The bay-head facies, with strong influence from rivers and salinity at normal times less than 6‰, has a very sparse fauna with only five macro-invertebrate species. In this environment ostracods dominate foraminifera (Ladd *et al.* 1957).

In enclosed bays of low to variable salinity (12–25‰) the characteristic feature is the occurrence of 'reefs' of *Crassostrea virginica*, the American estuarine oyster. The only other common lamellibranch on the reefs is the Mytilid *Brachidontes*. This association strongly recalls the *Liostrea hebridica–Modiolus* association which occurs both in the Hebrides and in the Upper Estuarine Series of the Midlands. *L. hebridica* is thought to be related to the modern *Crassostrea*. On the muddy bottoms between the reefs there are seven macro-invertebrates, including especially the small triangular lamellibranch *Mulinia lateralis*. This occurs in all environments, including some hypersaline ones and the open Gulf coast, but is most common in low salinities. Its behaviour is considered a good analogy for that of *Neomiodon*, which it somewhat resembles in morphology. In times of stable high salinities (> 25‰) these bays are invaded by the fauna normally characteristic of the more open bays nearer the inlets. This has far more species (34 according to Parker 1959), most of which also inhabit the open Gulf. Lamellibranchs and gastropods are still dominant. The assemblage at the algal bed horizon of the Lower Ostrea Beds is thought to be of this kind—a somewhat restricted selection of shallow water, open-sea forms typical of the Great Oolite limestones.

In his conclusion Parker reaffirms the classical account of the response of animals to adverse salinities, high or low. In unusual salinities there are few species, but many individuals. 'As salinity decreases or increases to normal values (along with relative stability), the number of species increases and the number of individuals per species decreases' (Parker 1959, p. 2158).

SALINITY-CONTROLLED ASSEMBLAGES IN THE GREAT ESTUARINE SERIES

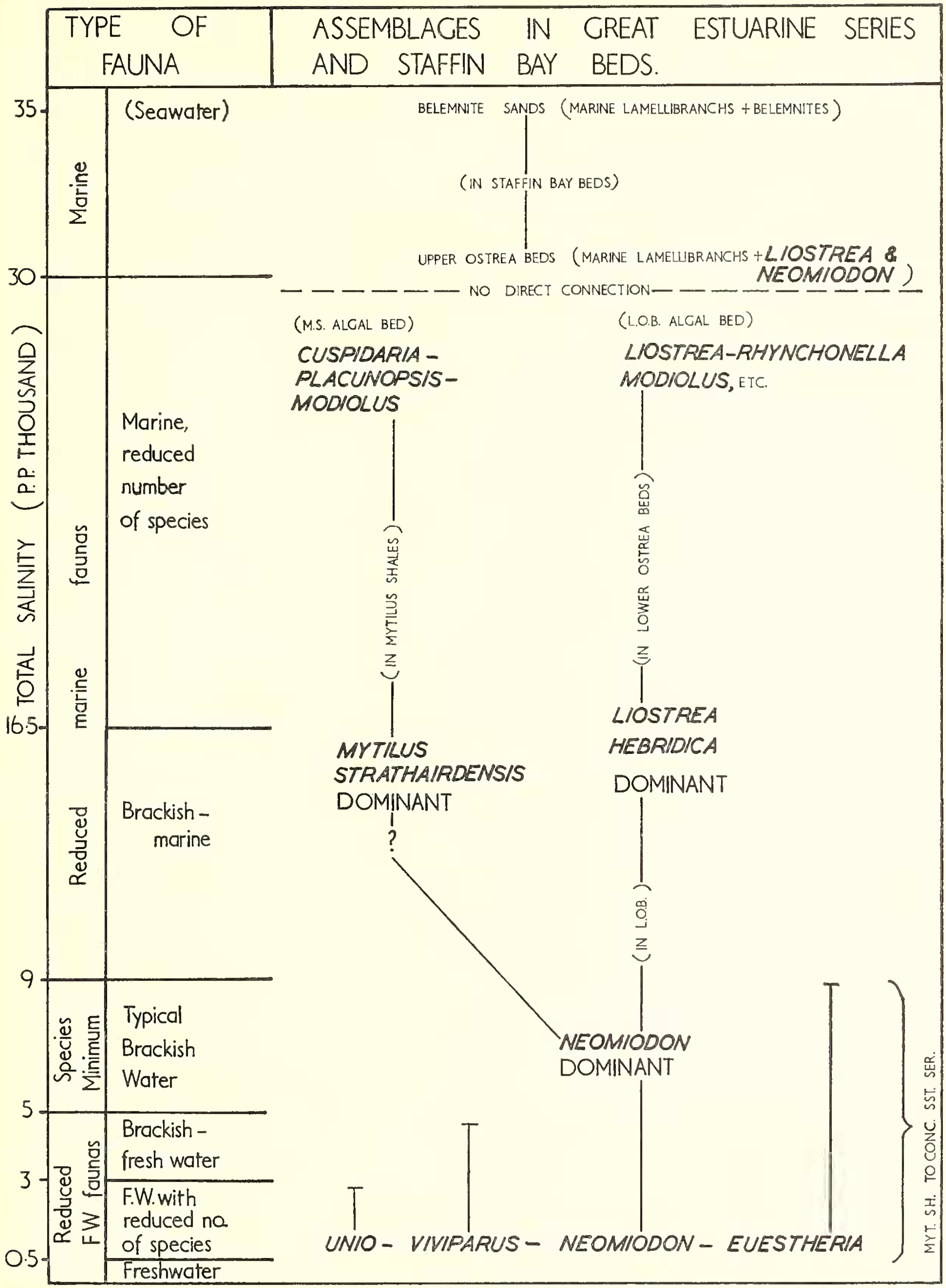
Rather a striking analogy can be drawn between the well-documented macro-faunal assemblages of the Texas Bays and those of the Great Estuarine Series. If such a system of bays and estuaries had existed in the Jurassic—and there is evidence independent of the fauna to show that it did in the Great Estuarine Series—it is reasonable to suppose that it would have been inhabited by assemblages of animals adapted to different salinity conditions, as in Texas today. I have argued that the general response of the fauna to salinity changes (relative numbers of species and individuals) should be similar, and that the estuarine genera concerned are likely to have been conservative ones. These are the general predictions, and direct comparison as outlined above shows that they are fulfilled.

Assuming actual mean salinity values for the habitats of the Jurassic assemblages having the best analogies with Recent ones, and using 'overlapping' of faunas for the others, I have constructed a 'salinity series' or spectrum for the Great Estuarine Series and Staffin Bay Beds (text-fig. 1). The principal values assumed are: *Unio–Viviparus–Neomiodon* = fresh water or less than 3‰; *Neomiodon* as only mollusc = the species minimum, 5–9‰; *Liostrea* dominant = *Crassostrea* reefs of Texas, 12–20‰; marine assemblage in Lower Ostrea Beds = open bays of Texas, more than 25‰; belemnites = marine, 35‰. The order which emerges does not involve reversing the salinity preferences of any of the surviving genera.

Several points must be made in qualification. (1) The order of the assemblages is obviously more certain than the actual salinity values assigned, which depend upon several assumptions (e.g. the salinity of the Jurassic ocean). (2) The values assigned are supposed to represent mean salinities; the salinity doubtless varied widely from time to time, as happens in Texas, but short-period oscillations have not usually been recorded in the fossil fauna. (3) The Jurassic assemblages are seen in vertical succession, and it is not possible as yet to prove lateral passage from one into another. However, except for the apparent extinction of *Mytilus strathairdensis*, there is little evidence of evolutionary change in the succession.

The salinity series presented is based entirely on the macrofauna, and especially on molluscs. Among the microfauna, ostracods are very abundant in what I regard as the low salinity (*Neomiodon–Viviparus–Euestheria*) assemblages of the Estheria Shales and Ostracod Limestones. I have not studied these, but Dr. F. W. Anderson informs me that they are mostly Metacyprids, which would not conflict with the interpretation given. Foraminifera are apparently absent from most of the Series, but have been seen in thin-sections and, as chitinous, decalcified shells, in microplankton separations, from the marine horizon of the Lower Ostrea Beds. A group of samples was examined for spores and microplankton by Mr. N. F. Hughes and Mr. R. N. Shrivastava. Most of the samples yielded spores and pollen, but only those from the Garantiana Clay (the bed immediately below the Great Estuarine Series), the Basal Oil Shale (a transition bed at the base of the Series), the two algal bed horizons, and the Staffin Bay Beds, yielded microplankton (dinoflagellates and hystrichospheres). Such microplankton is usually regarded as marine, and each of the samples yielding it had a marine or brackish-marine mollusc fauna.

Very few such salinity series have been constructed for fossil assemblages, and very few indeed from rocks as old as Jurassic. Schmidt (1951) quotes one, with some similarities to mine, prepared for Senonian rocks by Mertin (1939, unpublished thesis). Hiltermann (1949) has assigned salinity values to microfossil assemblages; some of these were criticized by Schmidt (1951). Less precise statements have often been made—marine-brackish, quasi-marine, &c.—not usually referred to any definition of the terms. Considerable scattered information of this sort exists on the Middle and Upper Purbeck Beds, which are in many respects similar to the Great Estuarine Series, but no synthesis has been published. By far the best-known non-marine rocks and faunas are those of the Coal Measures (Eagar 1960). Large salinity changes can be recognized both



TEXT-FIG. 1. Salinity-controlled assemblages in Middle Jurassic faunas. For explanation see text. Continuous lines show 'overlapping' of faunas in the formations indicated.

palaeontologically and geochemically, with consistent results (Ernst, Michelau, and Tasch 1960), but the effects of minor fluctuations in salinity are difficult to differentiate from the large effects of organic content, water turbulence, &c. (Eagar 1960, 1962). It would be surprising if further work did not extend, and in some respects complicate, the picture from the Great Estuarine Series, from which very little collecting has been done compared with the Coal Measures. But I am confident that the main thesis—that the faunas are brackish-water ones controlled mainly by salinity variations—is correct.

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